Table 2.1 *Soil crust lichens endemic to North America with both wide and limited distributions. Note that there are very few endemic species.*

Species	Distribution	Reference
Aspicilia californica	California Chaparral	Rosentreter 1998
Aspicilia filiformis	western North America	Rosentreter 1998
Aspicilia reptans	North America	Looman 1964
Catapyrenium congestum	Great Basin	Bruess and McCune 1994
Psora montana	western North America	Timdal 1986
Psora tuckermanii	Great Basin	Timdal 1986
Texosporium sancti-jacobi	western North America	McCune & Rosentreter 1992

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differential growth and erosion results in highly dissected pinnacles to 10 cm high (e.g., Colorado Plateau). Where freezing is common but soils are held in place with a heavy cover of lichens, mosses, and vascular plant roots, soil surfaces have a rolling rather than pinnacled topography (e.g., northern Great Basin). Where freezing is rare, crusts are flat when only cyanobacteria are present or rugose where lichens and/or mosses occur (e.g., the Sonoran Desert; Fig. 2.2, 2.3). In non-freezing regions, a layer of pebbles often covers cyanobacterial portions of the crust.

On the broad scale of western North America there are several different vegetation zones or ecoregions that contain biological soil crusts as major components (Fig. 2.1, Table 2.2, 2.3). The ecoregions used here are similar to those used by Bailey (1998). The most prevalent arid soils in North America are silt-loams and are more susceptible to physical disturbance than are clay-loams common to many other arid regions in the world, such as the red clay-loams of Australia.

2.2 Factors Influencing Distribution

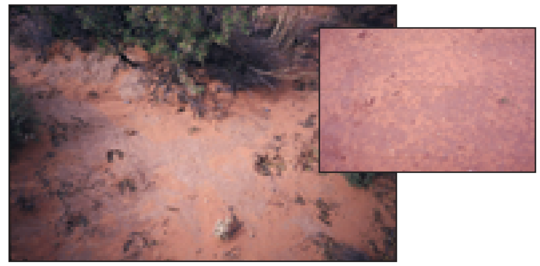
2.2.1 Elevation

Total crust cover is inversely related to vascular plant cover, as less plant cover results in more surface available for colonization and growth of crustal organisms (Fig. 2.4-A). Thus, when all crust types are combined (cyanobacterial, moss, lichen), cover is greatest at lower elevation inland sites (less than 1,000 m) compared to mid-elevation sites (1,000 to 2,500 m; Hansen et al. 1999; Fig. 2.4-B). However, relative lichen and moss cover increases with elevation and effective precipitation until vascular plant cover precludes their growth (Fig. 2.4-C). Crust organisms have reduced water and nutrient

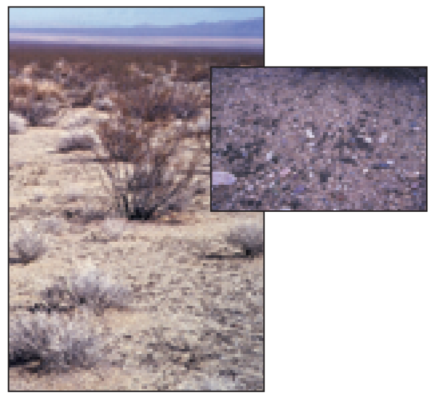
Figure 2.3 *Biological soil crust forms based on temperature characteristics of the environment.*

HOT DESERTS

flat

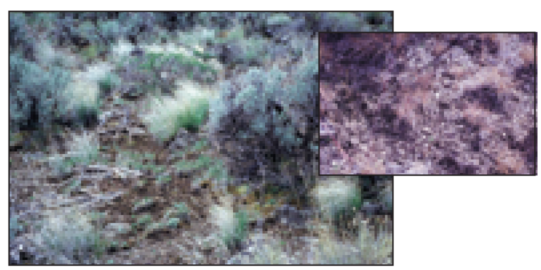


rugose



COOL DESERTS

rolling



pinnacled

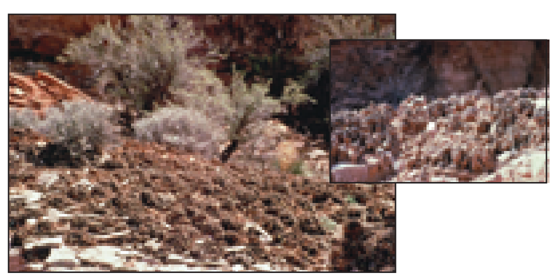


Table 2.2 *Soil, climatic, and vegetative characteristics for low and mid elevations in temperate North American arid and semi-arid ecoregions. Adapted from Bailey (*1995).

Ecoregion (Bailey's Ecoregion Province)	Dominant Soil Order	Soil Moisture/ Temperature	Average Annual Precipitation (mm)	Moisture Season/Form	Mean Annual Temperature Range (°C)	Predominant Evolutionary Disturbance	Vegetation Type
COOL DESERTS							
Columbia Basin (temperate semidesert)	mollisol	xeric/mesic	230-635	winter/rain spring/rain	4-14	drought	perennial grassland
Great Basin (temperate semidesert and desert)	aridisol	aridic/mesic to cryic	180-380	winter/snow spring/rain	4-13	drought	sagebrush steppe
Colorado Plateau (temperate semidesert and desert)	alfisol	xeric/thermic	205-510	winter/snow spring/rain summer/rain	4-13	drought	shrubland woodland
Great Plains (temperate steppe and dry steppe)	mollisol	ustic/mesic	485-735	winter/snow spring/rain summer/rain	8-15	fire, grazing	prairie
HOT DESERTS							
Mojave Desert (tropical/subtropical desert on sand)	aridisol	aridic/hyperthermic	100-150	winter/rain	13-29	drought	shrubland
Chihuahuan Desert (tropical/subtropical semidesert and desert on sand)	aridisol	aridic/thermic	205-325	summer/rain	10-18	drought	shrubland
Sonoran Desert (tropical/subtropical desert on sand)	aridisol	aridic/thermic	75-255	summer/rain fall/rain	10-24	drought	mixed thorn scrub
COASTAL CHAPARRAL							
California Chaparral (Mediterranean dry steppe)	mollisol	xeric/thermic	255-635	winter/rain	16-18	fire	chaparral

Table 2.3 *Dominant biological soil crust components and forms in North American arid and semi-arid ecoregions.*

Ecoregion	Dominant Biological Crust Components	Crust Morphology
Columbia Basin	tall mosses, green algae	rolling
Great Basin	moss, lichen	rolling
Colorado Plateau	non-heterocystic cyanobacteria *(Microcoleus)*, nitrogen-fixing lichens *(Collema)*	pinnacled
Great Plains	vagrant and foliose lichens	flat to rugose or rolling
Mojave Desert	non-heterocystic cyanobacteria *(Microcoleus)*, nitrogen-fixing lichens *(Collema)*, squamulose lichens, short mosses	flat to pinnacled
Chihuahuan Desert	heterocystic cyanobacteria *(Nostoc, Schizothrix)*, short moss	flat
Sonoran Desert	heterocystic cyanobacteria *(Nostoc, Schizothrix)*, gelatinous (nitroen-fixing) lichens (e.g., *Collema*), squamulose lichens, short mosses	flat
California Chaparral	heterocystic cyanobacteria *(Nostoc, Schizothrix)*, lichens, liverworts	flat

needs compared to vascular plants and can withstand the harsh growing conditions found in plant interspaces (Anderson et al. 1982a).

The positive relationship between biological crust cover and available soil surfaces has been amply demonstrated (Rogers 1972; Harper and Marble 1988; West 1990; Eldridge 1993b; Johansen 1993). As harsh environmental conditions limit vascular plant cover, greater cover of crusts in lower elevation sites probably occurs in spite of, not because of, these conditions.

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2.2.2 Soils and Topography

Stable or embedded rocks near or at the soil surface can increase the percent crust cover by perching water and armoring the surface from physical disturbances (Fig. 2.4-D). Shallow soils often support a wide variety of cyanobacteria, lichens, and mosses, regardless of soil texture (Fig. 2.4-E).

Soil texture heavily influences the species composition of biological crust communities. The more stable, fine-textured soils (such as gypsum and silty loams) support greater cover and more varied populations of cyanobacteria, lichens, and mosses (Fig. 2.4-F)

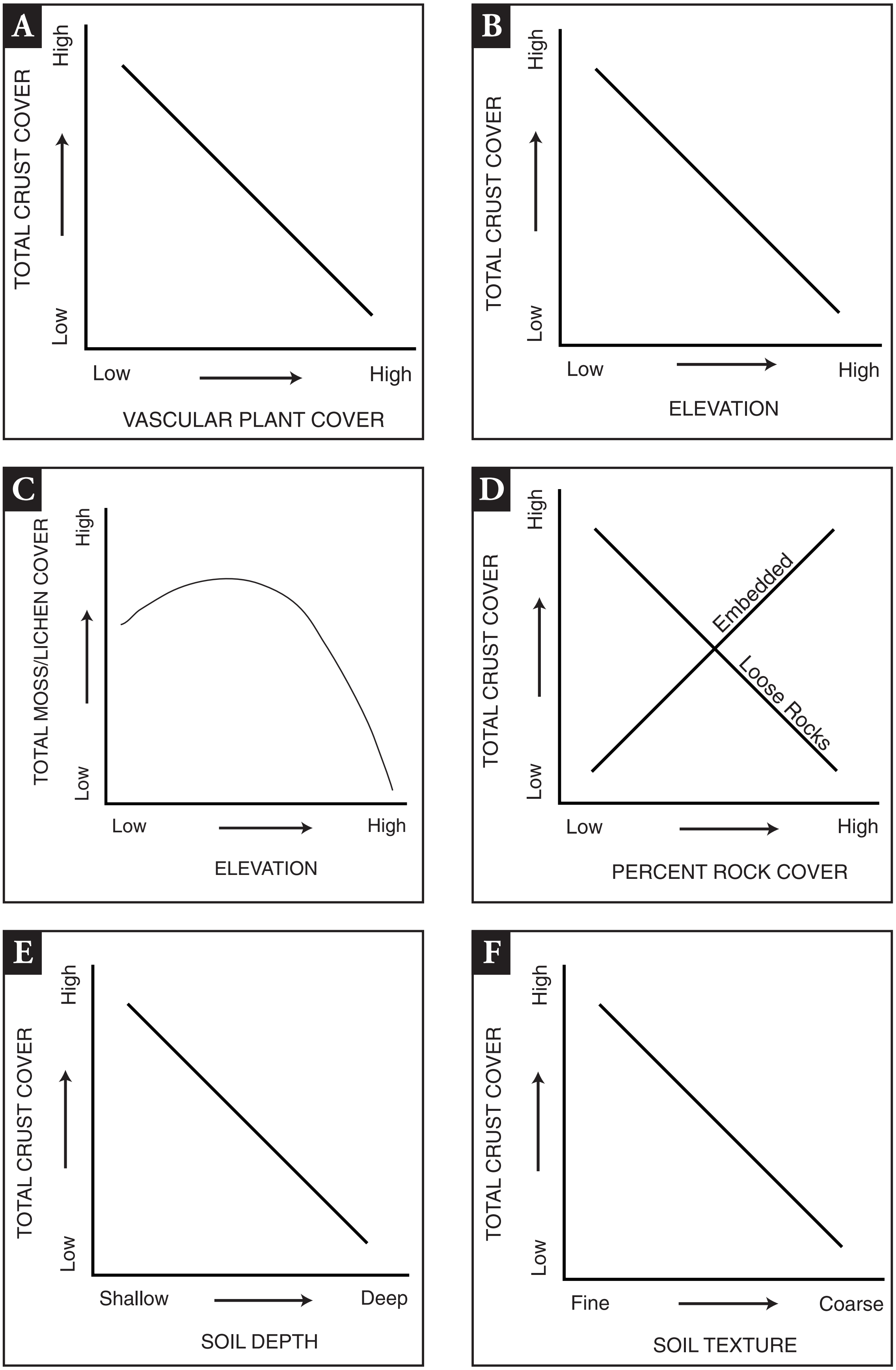

Figure 2.4 *General ecological relationships for biological soil crusts.*

than less stable, coarse-textured soils (Kleiner and Harper 1977b; Hansen et al. 1999). Coarse-textured soils may have only large filamentous cyanobacteria that are highly mobile (such as *Microcoleus*). However, once coarse-textured soils are sufficiently stabilized by larger cyanobacteria, other crustal organisms can then colonize, including smaller green algal and cyanobacterial taxa (such as *Scytonema* and *Nostoc*). Regardless of soil type, the first lichen to colonize is generally *Collema*, followed by *Placidium* (and *Caloplaca* in the northern Great Basin). In more unstable soils, lichens and mosses may be found only under vascular plants, where some protection from sediment burial is provided, or on north slopes, where greater moisture availability favors growth. Soil surface stability is influenced by texture (percent of sand, clay, silt), depth, and moisture content (wet, moist, dry). Sand and silt are more susceptible to surface disturbance when dry, while clay is highly stable (Fig. 2.5).

In later successional stages on stable surfaces, common lichen species include *Fulgensia bracteata*, *F. desertorum*, *Squamarina lentigera*, *Diploschistes muscorum*, and *Psora* spp. Common moss genera include *Tortula*, *Bryum*, and *Grimmia*. As soil stability increases, rich communities of cyanobacteria, lichens, and mosses become more widespread, covering all surfaces not occupied by vascular plants or rock.

Soil chemistry can also influence crust cover and composition. Calcareous and gypsiferous soils generally support high coverage of species-rich crust with some taxa being excellent indicators of soil chemistry (Table 2.4). Often physical crusts form stable surfaces that perch soil moisture, and given long periods without physical disturbance, will support both biological soil crusts and lichens or mosses normally found on rocks. Other abiotic factors that influence relative cover of microbiotic crusts are slope and aspect. Crustal organisms are only active when moist, and most active when warm. Therefore, north and east slopes generally favor crustal development in lower elevation desert regions. Slope angle does not generally affect crust cover or species richness, except where the slope or soils are unstable (Rosentreter 1986; Kaltenecker et al. 1997; Belnap and Bowker, unpublished data).

2.2.3 Disturbance

Intensity and type of soil surface disturbance, along with time since disturbance, influence the composition of biological crusts (see Chapter 4). The presence, absence, and abundance of early- or late-successional taxa can provide information regarding a site's disturbance history. This information, combined with data on vascular plant community composition, can assist the land manager in understanding a site's history, potential productivity, and ecological integrity.

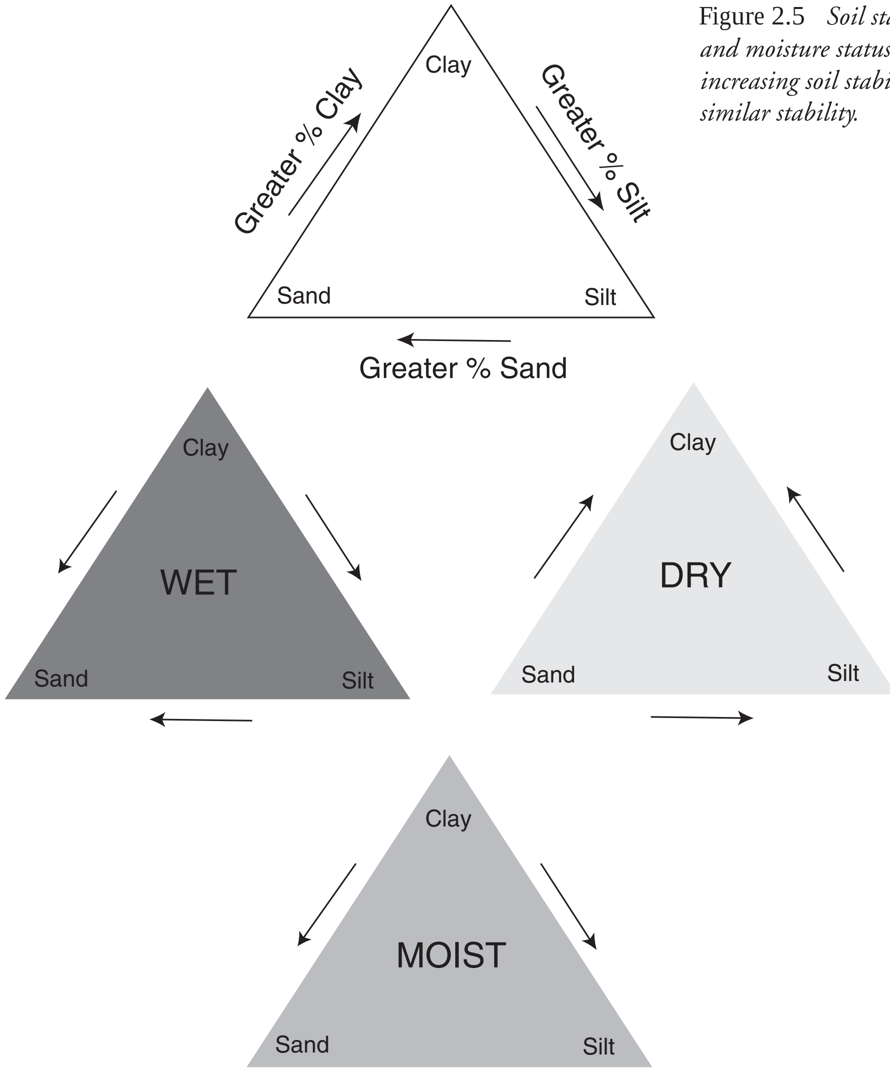

Figure 2.5 *Soil stability relative to texture and moisture status. Arrows indicate increasing soil stability. No arrow indicates similar stability.*

Soil Moisture Content	Soil Texture: Sand	Soil Texture: Clay	Soil Texture: Silt
Frozen	High	High	High
Wet	Medium-High	Low	Medium
Moist	Medium	Low	Medium
Dry	Low	High	Medium-Low

Table 2.4 *Soil crust lichens that are calcium carbonate indicators. Adapted from McCune and Rosentreter 1995.*

Low calcium carbonate	High calcium carbonate
Acarospora schleicheri	*Aspicilia fruticulosa*
Arthonia glebosa	*Aspicilia hispida*
Aspicilia reptans	*Buellia elegans*
Aspicilia filiforma	*Caloplaca tominii*
Cladonia borealis	*Collema tenax*
Diploschistes muscorum	*Fulgensia* spp.
Leptochidium albociliatum	*Heppia lutosa*
Megaspora verrucosa	*Phaeorrhiza nimbosa*
Ochrolechia upsaliensis	*Psora cerebriformis*
Placynthiella spp.	*Psora decipiens*
Psora nipponica	*Psora tuckermanii*
Xanthoparmelia wyomingica	*Toninia sedifolia*

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Intense disturbance results in bare soil. Severely, newly, or frequently disturbed soils are generally dominated by large filamentous cyanobacteria (Anderson and Rushforth 1976; Johansen et al. 1981, 1984; Johansen and Rushforth 1985; Harper and Marble 1988). When disturbance is less severe, less frequent, or some time has elapsed since the disturbance, crusts are generally in some mid-successional state, with some lichens and mosses present. Most of these species reproduce asexually, a life-history strategy that increases the probability of establishment (Rosentreter 1994). If disturbance continues, crusts will stay in early-successional stages (i.e., cyanobacteria only).

2.2.4 Timing of Precipitation

Dominance of biological crusts is highly influenced by seasonal precipitation patterns. Ecoregions that receive summer monsoons (e.g., the Sonoran Desert) tend to have a greater diversity of heterocystic cyanobacteria (such as *Lyngbya*, *Calothrix*, *Schizothrix*, and *Nostoc*) and lower lichen abundance. Lichens in these areas generally include the gelatinous genus *Collema* and squamulose genera *Placidium* and *Peltula* (Table 2.3). Large thalloid liverworts are more common in warm deserts than in the cool deserts of North America. In cool deserts, crusts are dominated by non-heterocystic cyanobacteria (such as *Microcoleus vaginatus*) and a diverse lichen flora, including *Acarospora schleicheri*, *Aspicilia* spp., *Candelariella*

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spp., *Collema* spp., *Diploschistes muscorum*, *Endocarpon pusillum*, *Placidium* spp., and *Psora* spp. These lichens physiologically prefer cool-season moisture and are adapted to lower light intensities common during winter months. The Columbia Basin, which receives more moisture and has more winter rain than the Great Basin, has a greater abundance of mosses than lichens (Ponzetti et al. 1998).

Biological soil crusts in regions influenced by fog, such as portions of the California Chaparral, support fruticose lichens that intercept moisture from the air (*Dendrographa* and *Schizopelte*). Biological crusts in many regions are best developed in interspaces between shrubs. In contrast, fog deserts show the best crust development under shrubs, due to the moisture intercepted by plant structure or by rock surfaces.

2.2.5 Vascular Plant Community Structure

The vertical and horizontal vascular plant structure of many arid and semi-arid vegetation communities optimizes growth of biological soil crusts. In cooler regions, greater structural diversity of vascular vegetation generally results in greater compositional diversity of biological crusts. Vascular plants create windbreaks and shade, influencing how much moisture and light reach the soil surface. They also trap leaf litter, keeping the interspaces free of substantial or persistent litter cover (Rosentreter and McCune 1992).

Invasive exotic plants generally decrease the structural diversity of native vascular plant communities by creating monocultures of densely spaced plants and by homogenizing litter distribution. They also lead to decreased biological crust cover and species richness in most ecosystems (Rosentreter 1994; Kaltenecker 1997). In addition, if moisture is retained under a litter layer for long periods while temperatures are warm, lichens can become parasitized by ubiquitous molds (Rosentreter 1984).

2.2.6 Ecological Gradients

Some lichens form natural replacement series along the same ecological gradients that influence vascular plants, although some lichen taxa are not good indicators of site conditions due to broad ecological amplitudes. For example, gelatinous lichens are most common in aridic calcareous sites and mesic non-calcareous sites (Fig. 2.6). Sites with frigid soil temperature regimes (mean annual temperature less than 8^{o}C) lack significant cover of gelatinous lichens. The genus *Leptogium* might be present; however, *Peltigera* and *Massalongia* tend to be more common. Some species display a shift in substrate preference in different ecoregions. For example, *Leptochidium albociliatum* occurs on mosses in the Great Basin, while in the Columbia Basin it is more common and occurs on bare mineral soil (Rosentreter 1986; Ponzetti et al. 1998).

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2.2.7 Microhabitats

Biological soil crusts can also create their own microstructure, which influences species distribution. Mosses create microsites that are very low in nutrients, low in calcium carbonate, and that retain moisture longer than bare mineral soil. This creates favorable sites for lichens that may benefit from the improved moisture regime and do not require many soil nutrients. Common examples include *Leptogium lichenoides*, *Massalongia carnosa*, and *Peltigera* spp. that grow only on mosses and are found in many sagebrush (*Artemisia*) steppe habitats.

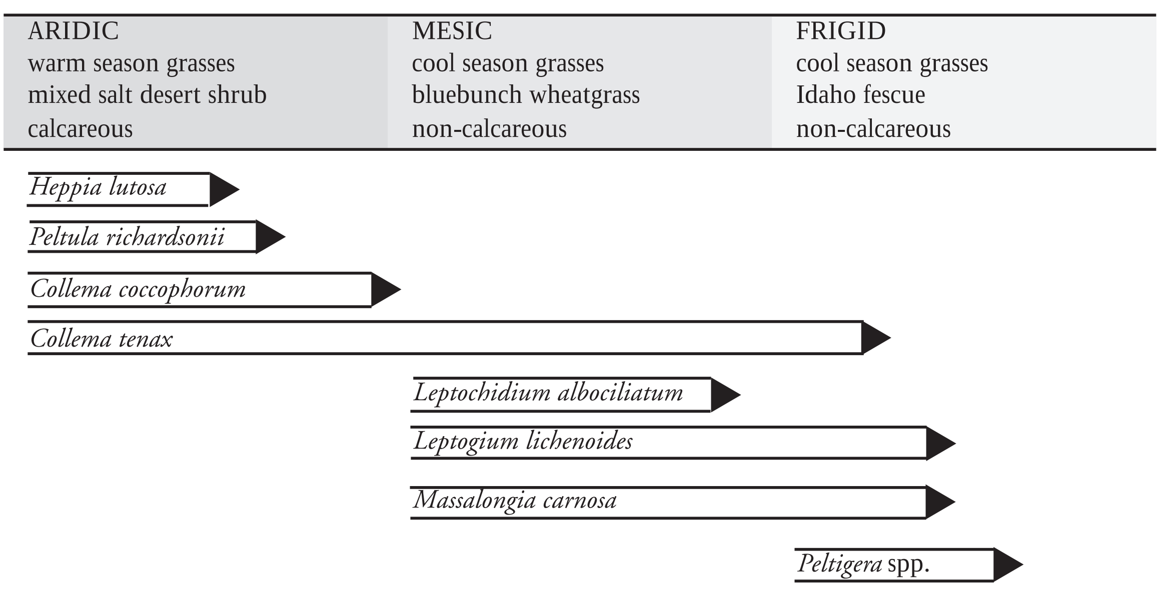
2.3 Unique Crustal Communities in North America

Special geologic features or soils create conditions that promote growth of biological soil crusts. Some of these sites support crusts containing uncommon associations or rare species. These unique crustal communities are not common across the landscape but are at times locally abundant. Some unique crustal communities are discussed below.

2.3.1 Gypsum

Gypsiferous outcrops are comprised of soils that are fine textured and have high concentrations of sulfate and calcium. Vascular plant cover at these sites is generally sparse with limited species diversity. Gypsiferous soils can support well-developed

Figure 2.6 *Gelatinous and other nitrogen-fixing lichens by relative soil temperature and calcareous influence.*



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biological crusts with a high lichen diversity (Anderson and Rushforth 1976; St. Clair et al. 1993), although sites in the hot deserts of the southwestern U.S. lack the species diversity of the cool deserts to the north. Common species include *Diploschistes diacapsis*, *Psora decipiens*, *Collema tenax*, *Placidium squamulosum*, *Buellia elegans*, and *Squamarina lentigera*. Several lichens are restricted to gypsiferous soils, including *Acarospora nodulosa* var. *nodulosa* (St. Clair and Warrick 1987), *Gypsoplaca macrophylla* (Timdal 1990), and *Lecanora gypsicola* (Rajvanshi et al. 1998). Gypsiferous sites are worthy of protection because of their high potential for cover and biological crust diversity. These sites are often threatened by mining activity due to the commercial value of gypsum.

2.3.2 Glades (Lithic and Shallow Soil Sites)

Glades are widespread across North America but are limited both locally and in overall area. Lithic and shallow soil sites are often colonized by biological crusts because these sites are extremely droughty and vascular plant growth is limited. In eastern forests, shallow disturbed or compacted soil (e.g., along roadsides) may be dominated by biological soil crusts, with *Baeomyces rufus* or *B. fungoides* often forming extensive crustal colonies. Pine barrens generally support extensive biological crusts. In western and more northern boreal forest openings, *Cladonia* spp., *Peltigera* spp., and occasionally *Multiclavula* spp. are dominant. These genera are also common on disturbed soil along roadways and cutbanks throughout the non-arid portions of the continent. Some lithic sites in wet climates are leached of soil nutrients and are often dominated by gelatinous lichens such as *Leptogium* or nitrogen-fixing cyanobacteria such as *Nostoc*.

2.3.3 Thermal Springs

Some parts of western North America contain extensive active or dormant thermal (hot) springs. Conditions in these areas are harsh, limiting vascular plant growth. Soil temperatures are often extremely high in summer and warm in winter. Soils containing thermal springs are often infertile, as warm water leaches many minerals, including calcium, magnesium, nitrogen, and phosphate. Toxic heavy metals can be present in the water and thus get deposited on the soil surface. These areas are covered with specialized thermic cyanobacteria when moist. When dry, they support either non-specialized biological crusts or crusts characteristic of gypsum.

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2.3.4 Cold Desert Playas

Small ephemeral pools form in parts of the Pacific Northwest where summers are hot and dry and winters are cool and moist (Rosentreter and McCune 1992). These sites are located on poorly drained basalt or other rock types, often barren of vascular vegetation and usually surrounded by some species of sagebrush (*Artemisia*). Drainage may be impaired by rock type or frozen soils, causing water to pond seasonally in flat, exposed areas. In late winter and early spring these sites experience cool, yet above freezing, temperatures for portions of the day. These conditions allow for slow evaporation of standing water. Such sites are sometimes referred to as playettes, as they are similar to but smaller than large seasonal lakes called playas. Playas support either attached or vagrant forms of *Dermatocarpon miniatum* and *Nostoc*. *Nostoc commune* found in these sites includes the common filamentous form, the colonial-eggs form, and occasionally the long, hair-like unattached form (referred to as var. *flagellaris*). Small playettes covered with fine silts can be colonized by *Nostoc* and by crustose lichens more typically occurring on rocks, such as *Lecanora muralis* (Rosentreter 1986).

2.3.5 Alpine Sod

Biological soil crusts are either dominant or common community components in many alpine and subalpine sites in North America. Alpine and subalpine sites contain some species common to the continent's arid regions. In contrast, a few lichens are characteristic of alpine crusts alone and include *Lecidoma demissum*, *Solorina* spp., *Lepraria neglecta*, *Ochrolechia frigida*, and *Thamnolia* spp. (DeBolt and McCune 1993). A genus that occurs on soil or rock in both alpine and arctic sites is *Stereocaulon*, which fixes nitrogen and is common worldwide in montane and alpine habitats (Lamb and Ward 1974). In the subalpine zone, biological crusts are often associated with areas where snowdrifts occur. Lichens characteristic of snow-patch sites are *Solorina crocea* and *Lepraria neglecta* (McCune 1998). Cyanobacterial crusts are also common in these areas and are generally dominated by *Nostoc* species (Reisiegl 1964).

2.3.6 Arctic Tundra

Alpine and tundra soils are often dominated by fruticose lichens (*Cladina* and *Cetraria*) and graminoids. Some areas are dominated by fruticose lichens that start out as crust communities in the early stages of succession. Tundra areas in North America have poor drainage due to frozen ground and are similar to other portions of the northern hemisphere, including Greenland. In some arctic regions there are also large areas of dry steppe-like vegetation, open

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Dryas heaths, and fell-fields with extensive coverage of biological crusts. Cyanobacterial crusts are commonly extensive and often dominated by *Nostoc* species (Hansen 1997).

2.4 Example: Biological Soil Crusts in Sagebrush Communities

Sagebrush species are common in western North America, particularly in the Great Basin and Columbia Plateau vegetation zones. Some of the same characteristics that influence sagebrush taxa distribution also influence biological crust development. Relative cover of biological crusts in various sagebrush vegetation types is presented in Table 2.5. Biological soil crusts tend to be lacking in sagebrush types that occur on seasonally flooded soils (silver, alkali, and fuzzy sagebrush; Winward 1980), as flooded soils create anaerobic conditions that are not well tolerated by lichens. Heavily saline soils also lack lichen cover, although moss is sometimes present if the salt concentration is not too great. Mountain, subalpine, and xeric big sagebrush types often lack significant biological crust cover due to dense vascular vegetation and accumulating plant litter. Other sagebrush types support higher biological crust cover unless soil surfaces are greatly disturbed or the current vegetation is in an early-successional stage.

Some lichens are good indicators of late-successional stages in sagebrush communities. The dual gradient theory proposed by McCune (1993) for lichen species succession in forested habitats applies well to arid and semi-arid regions in that species respond to time (age) and moisture in similar successional trajectories. Therefore, the length of time since the last major site disturbance or an increase in effective soil moisture will both provide suitable ecological conditions to support specific lichen species. This is why biological soil crust communities in different ecoregions recover at different rates (Table 2.2, Chapter 4).

Late-successional indicator species in sagebrush-steppe include *Acarospora schleicheri*, *Massalongia carnosa*, *Pannaria cyanolepra* (type b), *Trapeliopsis wallrothii*, *Trapeliopsis* sp. nov. (McCune, unpublished), and *Texosporium sancti-jacobi*. Some lichens are only present in late-successional communities because they grow upon other lichens or mosses. For example, *Acarospora schleicheri* grows upon *Diploshistes muscorum*, which in turn parasitizes the lichen genus *Cladonia*. Therefore, *Cladonia* can be considered a keystone organism influencing a site's diversity. *Massalongia carnosa* primarily grows on mosses and is not present until mosses become well established within a site. *Texosporium sancti-jacobi* is restricted to old-growth sagebrush communities and occurs only on decaying organic matter (McCune and Rosentreter 1992). Other lichens that commonly occur on decayed organic matter but are not restricted to old-growth sites include *Buellia papillata*, *B. punctata*, *Caloplaca* spp., *Lecanora* spp., *Megaspora verrucosa*, *Ochrolechia upsaliensis*, *Placynthiella* spp., and *Phaeophyscia decolor*.

Table 2.5 *Relative cover of biological soil crusts in sagebrush (Artemisia) vegetation types.*

HIGH biological crust cover	LOW biological crust cover
Tall Sagebrush	
Wyoming big sagebrush *(A. tridentata* ssp. *wyomingensis)*	subalpine big sagebrush *(A. tridentata* ssp. *spiciformis)*
basin big sagebrush *(A. tridentata* ssp. *tridentata)*	xeric big sagebrush *(A. tridentata* ssp. *xericensis)*
mountain big sagebrush** *(A. tridentata* ssp. *vaseyana)*	mountain big sagebrush** *(A. tridentata* ssp. *vaseyana)*
	silver sagebrush *(A. cana)*
	three-tip sagebrush *(A. tripartita)*
Short Sagebrush	
low sagebrush *(A. arbuscula)*	alkali sagebrush *(A. longilobia)*
black sagebrush *(A. nova)*	fuzzy sagebrush *(A. papposa)*
stiff sagebrush *(A. rigida)*	
Bigelow sagebrush *(A. bigelowii)*	
fringed sage *(A. frigida)*	

**Biological crust cover high or low depending on site characteristics.